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Relation of leaf micromorphology with photosynthesis and water efflux in some Indian mangroves

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Stomatal size and frequency, cuticle thickness and the amount of mesophyll tissues were measured in leaves of 14 mangrove species belonging to seven families of the Sundarbans vegetation. The rate of assimilation and water efflux were estimated *in vitro*. In this tropical estuary high salinity prevails in soil and water, hence the dominating mangrove vegetation develops some morpho-anatomical adaptations to cope with such adverse ecology. Some architectural parameters of leaves have a significant relation with carbon assimilation and water-use characteristics. In all the studied taxa, photosynthesis is positively correlated to stomatal frequency and the amount of mesophyll tissue, while an inverse relation exists with stomatal size. Similarly, transpiration and stomatal conductance directly correlate to the abundance of stomata, but reciprocate to their size. Cuticle thickness is inversely related to transpiration, but hardly any relation was noticed with the rate of photosynthesis and stomatal conductance. The amount of mesophyll tissue has a direct relation with carbon assimilation, while its effect upon transpiration and stomatal conductance seems to be insignificant.

Keywords: Leaf, anatomy, mangrove, photosynthesis, stomatal conductance, transpiration.

Introduction

The architecture, especially the micromorphology, of mangrove leaves has drawn much attention time to time (SESHAVATHARAN and SRIVALLI 1989, FITZGERALD et al. 1992, DAS and GHOSE 1993, RAMASSAMY and KANNABIRAN 1996, DAS 1999). But structural information in terms of function is rare and mostly based on assumptions rather than experimental evidence. TOMLINSON (1986) opined that it is the suite of functional characteristics that allows mangroves to survive in saline environments. It is obvious that the structural characterization must have some functional explanations: cuticle, mesophyll zone and the stomatal characteristics relate to transpiration and photosynthesis; salt glands and water storage tissue are attributed to the maintenance of salt balance and the increased number of vessel elements per unit area is related to water stress. Recent data from diverse fields have established the importance of the morphology of stomata, their distribution and behaviour

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as constraints of a spectrum of plant physiology and global ecology (MALIK and BHOSALE 1983, BEERLING and KELLY 1997, PAOLETTI et al. 1998, LIN et al. 2001, XIE and LUO 2003).

In the tidal wetlands along tropical and sub-tropical coasts high salinity forces the dominating mangrove vegetation to cope with physiologically dry soil. In such a condition, these plants restrict transpiration rates by regulating stomatal conductance (NANDY and GHOSE 2001). On the other hand, reduced stomatal conductance restricts CO_2 influx in leaf cells, thereby limiting the rate of net photosynthesis in mangroves (CHEESEMAN et al. 1991, NANDY and GHOSE 2001). Thus, the rate of carbon assimilation and water efflux are influenced by stomatal conductance, which in turn, is regulated by the size and frequency of stomatal apertures. Thickness of cuticle may affect the exposure of thylakoid membranes to sunlight and thus controls the rate of carbon assimilation. The presence of thick cuticle in mangrove leaves is more or less a constant feature, to reduce excess loss of water (DAS 1999). Moreover, in most mangroves, non-chlorophyllous water storage tissue encroaches on the area of the mesophyll zone and occupies good amount of the total leaf thickness. Thereby, the rate of net photosynthesis may be reduced to some extent. Experimental evidence has proved that *Rhizophora mangle* adjust their leaf morphology, photosynthetic rates and nutrient uptake in response to changing resource availability (CHOONG et al. 1992, BALL 1996). However, factors affecting photosynthesis in mangroves have yet been little understood (KATHIRESAN and MOORTHY 1993, 1994), especially the dependence of photosynthesis on leaf anatomy. In view of this, the present work aims to determine the relationship between some physiological parameters (*viz.* photosynthesis, stomatal conductance and transpiration) and corresponding leaf architecture (*viz.* stomatal size, abundance, cuticle thickness and amount of mesophyll tissue), if any.

Materials and methods

14 species from seven families of typical mangroves (Tab. 1) from the Sundarbans forest have been dealt with. Physiological parameters such as, photosynthesis, stomatal conduc-

Tab. 1. List of the species studied with family names

Species studied	Family
Aegiceras corniculatum (L.) Blanco.	Myrsinaceae
Aegialitis rotundifolia Roxb.	Plumbaginaceae
Avicennia alba Bl.	Avicenniaceae
A. marina (Frosk) Vierh.	Avicenniaceae
A. officinalis L.	Avicenniaceae
Bruguiera gymnorrhiza L. (Lam.)	Rhizophoraceae
B. parviflora W. et A.	Rhizophoraceae
Ceriops decandra (Grif.) Ding. Hou.	Rhizophoraceae
C. tagal (Pierre.) Robins.	Rhizophoraceae
Heritiera fomes Buch. Ham.	Sterculiaceae
Nypa fruticans (Thunb.) Wurmb.	Arecaceae
Phoenix paludosa Roxb.	Arecaceae
Xylocarpus granatum Konig.	Meliaceae
X.mekongensis Pierre.	Meliaceae

tance and transpiration were measured *in situ* under broad day light condition (800–2000 µmol PHOTONS $m^{-2}s^{-1}$ PAR) using an infrared CO_2 Gas Analyser (PS 301 CID, USA) equipped with an open chamber. Ten consecutive measurements from a single plant were taken for each parameter. Stomatal size and frequency per mm^2 were estimated from epidermal peelings. Thickness of the entire leaf, cuticle and mesophyll zone were measured from thin hand sections after proper staining (JOHANSEN 1959). Mesophyll ratio was calculated by taking the thickness of the entire leaf and the mesophyll zone into account. An average of 20 random observations was taken from five plants of each species for each parameter and correlation values were calculated between the estimated physiological data and anatomical characteristics using the Microsoft Excel package. Some representative photomicrographs of the leaf sections are also provided herewith (Fig.1)

Results

In all the investigated taxa, except in *Phoenix paludosa*, leaves are dorsiventral with stomata scattered on their abaxial surface. In *Phoenix paludosa*, the leaf is isolateral, but stomata are abaxially distributed. In most of the species, the stomata are sunken, with a sub-stomatal chamber (Fig. 1B, D, G, K). Guard cells often have beak-like cuticular outgrowths (ledges) either at the outer side or at both the inner and the outer side of the stomatal pore (Fig. 1B, D, J, K). Stomatal size ranges from 0.317mm (*Xylocarpus mekongensis*) to 1.46 mm (*Nypa fruticans*) (Fig. 2). Stomatal frequency/ mm^2 is highest in *Heritiera fomes* (646) and *X. mekongensis* (643) and lowest in the genus *Bruguiera* (125 in *B. gymnorrhiza* and 134 in *B. parviflora*) (Fig. 3). In general, the cuticular surface is uninterrupted and smooth. In *Heritiera fomes*, presence of stellate hairs on the abaxial surface and in *Avicennia* sp. abaxially grown uniseriate capitate hairs interrupt the cuticle (Fig. 1E, I); in *Aegialitis rotundifolia*, however, an uneven deposition is noticed in the cuticular layer (Fig. 1A). The cuticle is considerably thin in *N. fruticans* (0.032mm), *P. paludosa* (0.033 mm) and *X. mekongensis* (0.039 mm), while quite thick in *Aegiceras corniculatum* (0.009mm), *Avicennia* spp. (0.004–0.008 mm), *Bruguiera* spp. (0.014–0.059mm) and *Ceriops decandra* (0.089 mm) (Fig. 2). In most of the species, the mesophyll comprises a few layers of compact, anticlinally extended thin-walled palisade and loosely arranged isodiametric spongy parenchyma (Fig. 1). In *Heritiera fomes,* palisade cells are poorly developed and traversed by large intercellular spaces (Fig. 1I). The photosynthesising chlorophyllous zone is quite wide in *P. paludosa* and *B. parviflora,* where the mesophyll ratios are 0.92 mm^{-1} and 0.87 mm^{-1} respectively. On the other hand, rather narrow mesophyll was noticed in *A. corniculatum* and *X. mekongensis*, the ratios being 0.38 and 0.32 respectively (Fig. 2).

The rate of net photosynthesis ranges between 3.69–8.62 µmol CO_2 m^{-2} s^{-1} in most of the studied taxa (Fig. 4). An abrupt rise was noticed in *Heritiera fomes* where photosynthesis is as high as 13.21 µmol CO_2 m^{-2} s^{-1}. Among the others, the assimilation rate is signfiicantly high (>8 µmol CO_2 m^{-2} s^{-1}) in *Avicennia officinalis*, *Aegiceras corniculatum*, *Aegialitis rotundifolia* and *Xylocarpus granatum*, while considerably low photosynthesis (< 4 µmol CO_2 m^{-2} s^{-1}) was measured in *Ceriops decandra* and *Phoenix paludosa* (Fig. 4). Interestingly, stomatal conductance is also minimal in the latter species (39.23 and 30.23 mmol H_2O m^{-2} s^{-1} respectively). Significantly high stomatal conductance (> 100 mmol H_2O m^{-2} s^{-1}) was estimated in *A. alba, A. marina, A. corniculatum, B. gymnorrhiza, H.*

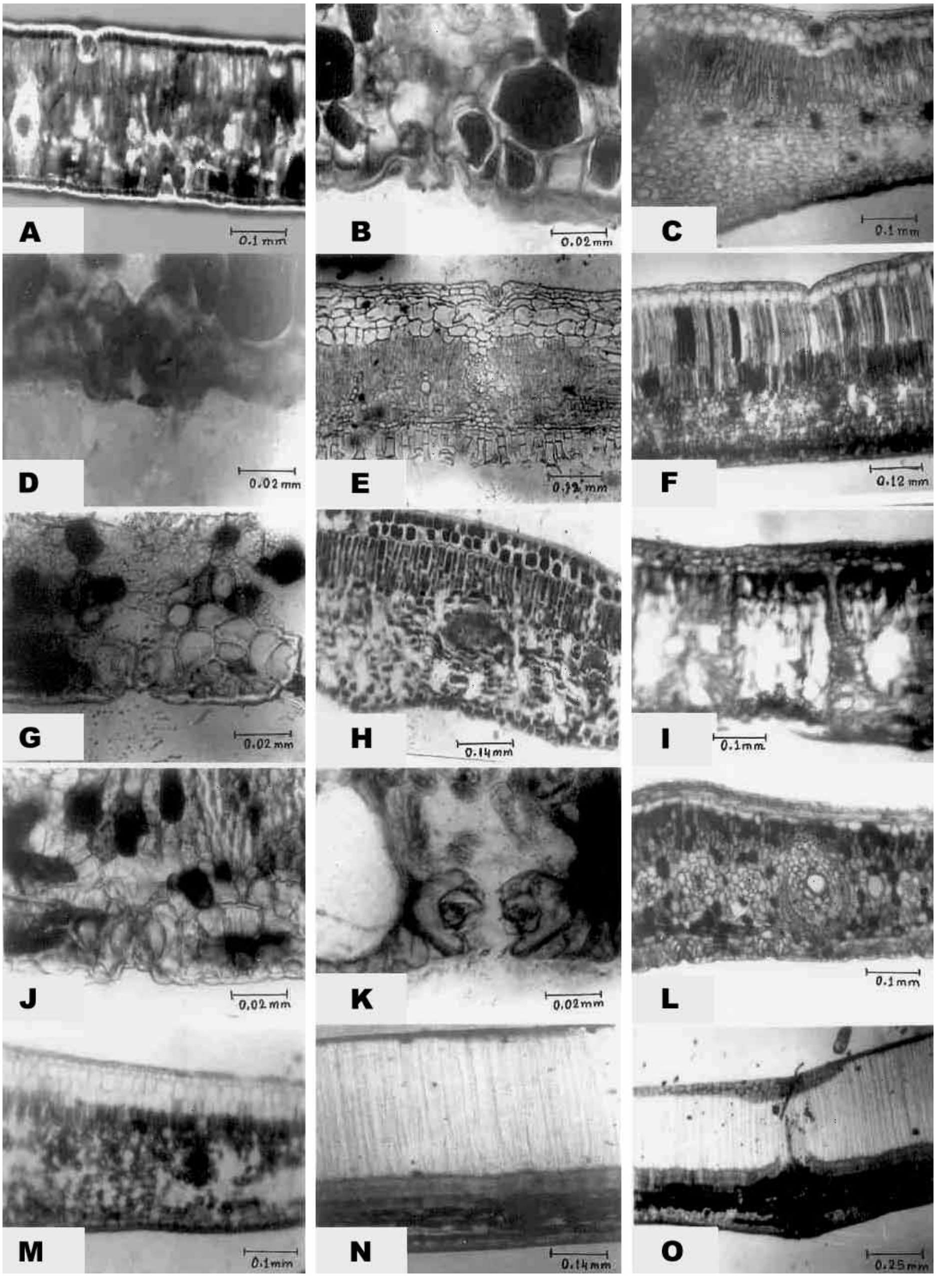

Fig. 1. A-O Transverse sections of leaves of some representative mangroves. A-B *Aegialitis rotundifolia*; A Leaf section, B Sectional view of stomata. C-D *Aegiceras corniculatum*; C Leaf section, D Sectional view of stomata, E Leaf section of *Avicennia alba*. F-G *Bruguiera gymnorrhiza*; F Leaf section, G Sectional view of stomata. H Leaf section of *B. parviflora*, I Leaf section of *Heritiera fomes*. J-K Sectional view of stomata; J *Nypa fruticans*, K *Phoenix paludosa*. L Leaf section of *Nypa fruticans*. M Leaf section of *Rhizophora mucronata*. N Leaf section of *Xylocarpus granatum*. O Leaf section of *X. mekongensis*

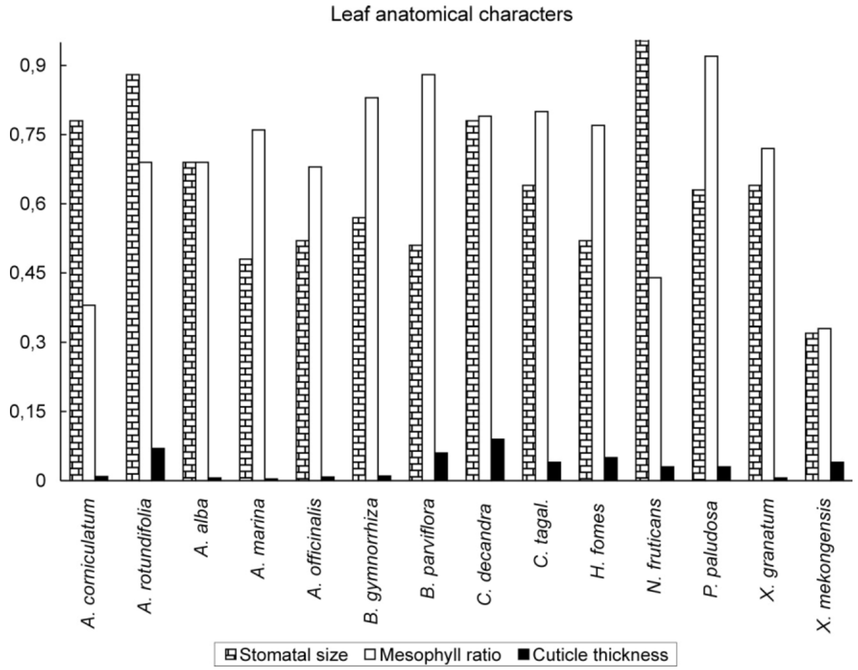

Fig. 2. Micromorphological parameters of the studied leaves. Stomatal size (mm), mesophyll ratio and cuticle thickness (mm).

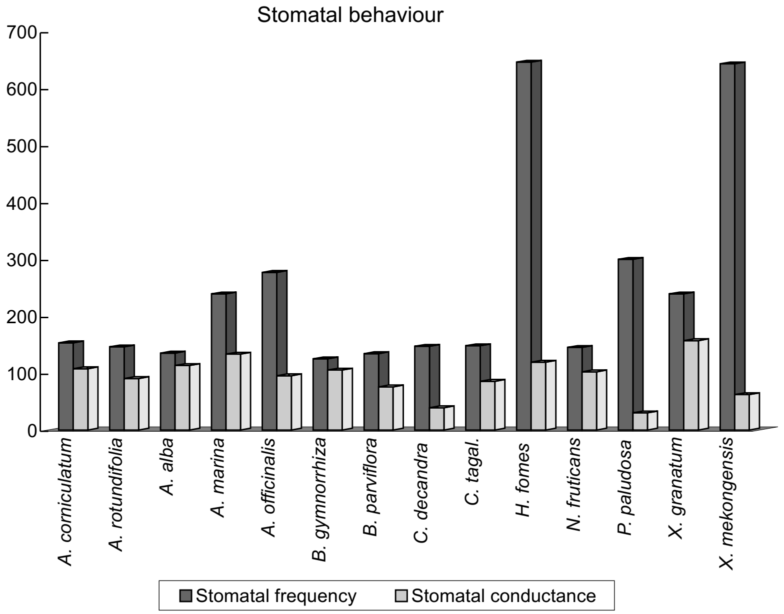

Fig. 3. Stomatal frequency mm^{-2} and stomatal conductance (mmol H_2O m^{-2} s^{-1}) of the investigated taxa

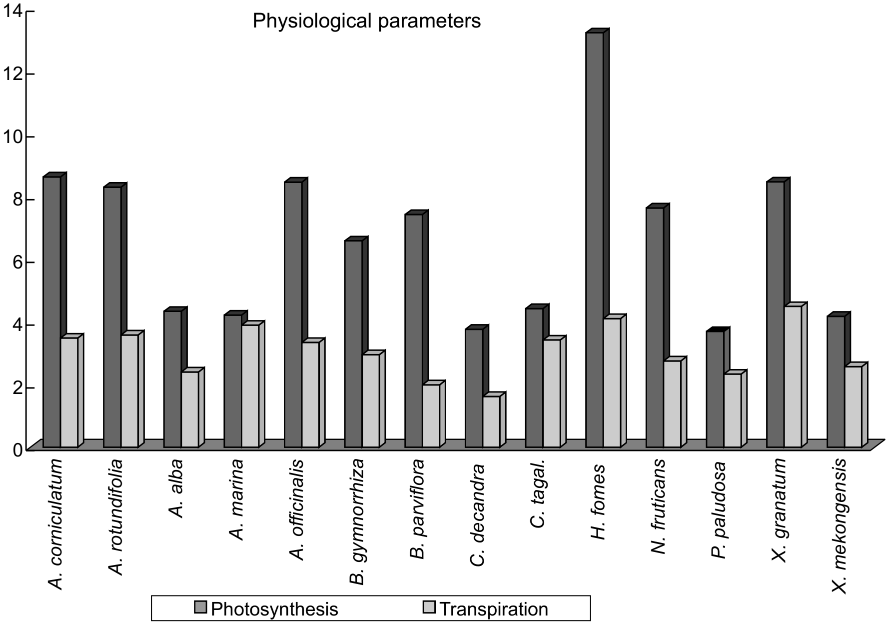

Fig. 4. Rate of net photosynthesis (µmol CO_2 m^{-2} s^{-1}) and transpiration (mmol H_2O m^{-2} s^{-1}) of the investigated taxa.

fomes, N.fruticans and *X.granatum* (Fig. 3). The rate of transpiration ranges between 1.62–4.49 mmol H_2O m^{-2} s^{-1} amongst the studied taxa. Water efflux is considerably low (< 2 mmol H_2O m^{-2} s^{-1}) in *B.parviflora* and *C.decandra*, but quite high (> 3.5 mmol H_2O m^{-2} s^{-1}) in *A. marina, A.rotundifolia*, *H. fomes* and *X.granatum* (Fig. 4).

Correlation values (R – value) were calculated from the available physiological data and the anatomical characters of the leaves. In all the studied taxa, photosynthesis correlates inversely with stomatal size (–0.99 to –0.61) but strong positive correlation exists with stomatal frequency (0.97 to 0.63) and mesophyll ratio (0.97 to 0.67). The lowest correlation with stomatal frequency and mesophyll ratio was obtained in *H. fomes* (0.63 and 0.67 respectively). Cuticle thickness, however, shows hardly any relation with photosynthesis (Table 2). Transpiration has the same trend of correlation with stomatal size (–0.97 to –0.65) and frequency (0.95 to 0.65), but a remarkably inverse correlation exists with cuticle thickness (–0.99 to –0.6) (Table 2). The lowest correlation value between cuticle thickness and transpiration was obtained in *P. paludosa* (0.6). Stomatal conductance and frequency of stomata/ mm^2 are positively correlated (0.98 to 0.69), whereas, the size of stomatal apertures reciprocate to stomatal conductance (–0.98 to –0.61). Neither transpiration nor stomatal conductance relates to the amount of mesophyll tissue. Stomatal conductance seems unaffected by the thickness of cuticle (Tab. 2).

Discussion

The magnitude of photosynthesis largely depends on the physical characteristics of leaf i.e. on stomatal apertures that play an active role in photon trapping and CO_2 influx from

Tab. 2. Correlation values of some anatomical characterrs with their physiological parameters (Ss – Stomatal size, Fs – Stomatal frequency, Tc – Cuticle thickness, Mr – Mesophyll ratio)

Species	R- values											
	Photosynthesis				Transpiration				Stomatal conductance			
	S_s	F_s	T_c	Mr	S_s	F_s	T_c	Mr	S_s	F_s	T_c	Mr
Aegiceras corniculatum	–0.88	0.75	–0.4	0.92	–0.79	0.75	–0.62	0.6	–0.84	0.5	–0.86	0.64
Aegialitis rotundifolia	–0.8	0.88	–0.17	0.9	–0.84	0.65	–0.94	0.56	–0.84	0.6	0.5	–0.15
Avicennia alba	–0.77	0.68	0.37	0.84	–0.74	0.76	–0.74	0.39	–0.71	0.67	–0.34	0.29
A. marina	–0.94	0.86	0.32	0.94	–0.96	0.8	–0.88	0.83	–0.74	0.85	0.23	0.92
A. officinalis	–0.82	0.68	–0.2	0.91	–0.85	0.75	–0.86	0.72	–0.74	0.84	0.23	0.09
Bruguiera gymnorrhiza	–0.89	0.73	–0.05	0.81	–0.77	0.79	–0.94	0.81	–0.78	0.7	–0.29	0.41
B. parviflora	–0.93	0.62	–0.03	0.89	–0.72	0.67	–0.61	0.22	–0.87	0.84	–0.09	0.59
Ceriops decandra	–0.99	0.86	0.09	0.86	–0.97	0.63	–0.99	0.63	–0.98	0.89	–0.87	0.89
C. tagal	–0.96	0.96	0.42	0.97	–0.76	0.76	–0.75	0.98	–0.81	0.83	–0.69	0.99
Heritiera fomes	–0.87	0.63	–0.15	0.67	–0.72	0.83	–0.75	0.46	–0.85	0.78	–0.53	0.58
Nypa fruticans	–0.61	0.86	–0.06	0.77	–0.73	0.89	–0.75	0.59	–0.88	0.59	–0.25	0.22
Phoenix paludosa	–0.82	0.7	0.43	0.97	–0.85	0.9	–0.6	0.45	–0.63	0.9	–0.19	0.98
Xylocarpus granatum	–0.74	0.59	0.16	0.9	–0.76	0.95	–0.79	0.51	–0.66	0.98	–0.24	–0.38
X.mekongensis	–0.81	0.61	0.09	0.79	–0.65	0.76	–0.84	0.66	–0.61	0.8	–0.36	0.68

the ambient to the internal atmosphere. The opened stomata also provide a route for water efflux by transpiration. Thus, stomata are the sole factor responsible for the energy and water balance in the plant body.

The larger the size of stomata, the less their abundance per unit area (DAS and GHOSE 1993) and the functional pore density for gas exchange is dropped. The rate of photosynthesis, therefore, has a strong positive correlation with stomatal frequency, but reciprocates to the size of apertures. SCHLUTER et al. (2003) experimentally showed that increased stomatal density in *Arabidopsis* mutant (sdd1-1) enables it to have a 30% higher CO_2 assimilation rate than the wild type. A positive correlation between net photosynthesis and stomatal frequency was also observed in *Azadiracta indica* (KUNDU and TIRESTEDT 1999). Chloroplast is the ultimate reaction site for carbon assimilation that points to a significant positive correlation between photosynthesis and the total amount of chlorophyllous mesophyll tissue in the leaf. XIE and LUO (2003) found that increase in mesophyll thickness provides greater production of carbohydrates. Experimental evidence suggests that in *Bruguiera parviflora*, NaCl has a limiting effect on photochemistry, which ultimately affects photosynthesis by inhibiting chlorophyll synthesis (50% loss in chlorophyll) (PARIDA et al. 2004).

A high saline condition prevails at the natural mangrove habitat, and to cope with the physiologically dry soil, the mangrove leaf reduces the transpiration rate by restricting stomatal conductance (NANDY and GHOSE 2001). Simultaneously, photosynthesis is remarkably lower in mangroves, as reduced stomatal conductance is unfavourable for CO_2 influx into the leaf cells (CHEESEMAN et al. 1991). At the threshold of desiccation, the cuticular layer is the ultimate barrier between the plant and atmosphere. In mangroves, the rather thick cuticle plays an active role in restricting non-stomatal water loss (DAS 1999) and the cuticular outgrowths either at the outer side or at both the outer and inner sides of the stomatal pore (ledges) provide some device to minimise water loss through stomata (DAS and GHOSE 1993). This may explain the significant inverse relation between cuticle thickness and transpiration. The present study supports the view of SANTRUCEK et al. (2004) that resistance to flux of water through solid cuticle on the stomatous leaf surface was about 11 times lower than cuticular resistance on the astomatous leaf surface. This indicates pronounced difference in barrier properties between cuticles isolated from both leaf surfaces.

FARQUHAR (1978) opined that the stomata react to photosynthesis through a feedback link: they open at low internal CO_2 concentration. The present observation contradicts the view of NOBEL (1991) that conductance is proportional to the square of the effective radius of the stomatal pore. According to him, as a potential developmental response to CO_2 starvation, the increased stomatal size facilitates CO_2 diffusion into the leaf. In fact, due to respiration, as CO_2 partial pressure decreases inside the leaf cells, stomata need to be opened for CO_2 influx, which requires profuse number of stomata on the leaf surface. The degree of stomatal opening is therefore significantly determined by stomatal frequency (positive). Conversely, large stomata point to their lower frequency per unit area of leaf. Thus, the pore size reciprocates to stomatal conductance. Experimental evidence in Ponderosa Pine by HUBBARD et al. (2001) proved that stomatal conductance decreases with increasing stomatal size.

In *Heritiera fomes*, although a high assimilation rate can sometimes be measured, it is not consistently maintained. NANDY and GHOSE (2001) reported that in *Heritiera* the optimum irradiance required for maximum photosynthesis is 1210 µmol PHOTONS $m^{-2}s^{-1}$, whereas more than 2000 µmol PHOTONS m^{-2} s^{-1} PAR is available in the Sundarbans forest on a bright sunny day. This can be explained by poorly developed mesophyll tissue and the lower correlation values between photosynthesis and stomatal frequency, so that despite a high density of stomata, the photosynthesis rate is not very high throughout the day. In addition, the rather thin cuticle can be hypothesised to allow the high transpiration rate (Fig. 2A,C) that makes the species incompatible with growth in the highly saline and physiologically dry soil condition of western Sundarbans. An earlier report by CHANDA and DATTA (1986) also supports this view and attention is needed to save this threatened species from the disastrous impact of increased salinity in the western Sundarbans.

Thus, leaf micromorphology has definite impact on the carbon assimilation and water efflux of mangroves. The correlation of photosynthesis with size and frequency of stomatal apertures and volume of mesophyll tissue helps these plants to avoid high light intensities and extremely high ambient temperature, but to maintain carbon assimilation at a consistent rate throughout the day. Photoinhibition was, therefore, not reported in mangroves (CHEESEMAN et al.1991, CHEESEMAN 1994). On the other hand, thickness of cuticle and stomatal size controls the rate of transpiration which, in turn leads to leaf succulence, an essential adaptation under salt stress.

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